

THE VASCULAR FLORA OF LA SELVA BIOLOGICAL STATION, COSTA RICA* CECROPIACEAE

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Dioecious trees, sometimes epiphytic; trunk often straight, slender and with branches only well above the middle; branches and trunk with conspicuous stipular scars; adventitious roots present; sap watery or resinous. *Leaves* clustered at the tips of branches, spirally arranged, simple and entire to deeply, palmately lobed; lateral veins very regularly spaced; tertiary veins regular, closely parallel and perpendicular to the lateral veins; stipules large, fused and encircling the stem; blades, branches and stipules usually scabrous. *Inflorescences* paired in the axils of leaves, compound clusters of corymbs, heads, or spikes or the inflorescences unbranched and the flowers sessile at the end of the peduncle. *Staminate flowers* with a 2-4-lobed perianth and 2-4 stamens; *pistillate flowers* with a 2-4-lobed perianth or the tepals fused into a tube covering the ovary except for the apical stylar opening; ovary simple, the ovule basal; stigma 1. *Fruit* achene-like or drupaceous.

The Cecropiaceae contain 200-300 species in six genera of which three are endemic to the neotropics and three to the paleotropics. These six genera have often been treated as a subfamily of the Moraceae, but are perhaps more closely related to the Urticaceae with which they share solitary stigmas and basally attached ovules. Following Berg (1978) they are here treated as a separate family. The Urticaceae are mostly monoecious herbs and all have incurved elastic stamens that snap out, releasing pollen at anthesis; the Cecropiaceae are all strictly dioecious shrubs

or trees and have more or less straight nonelastic stamens.

KEY TO THE GENERA

1. Leaves peltate, palmately lobed; inflorescences pendent umbels of long, densely flowered spikes; plants providing internally both shelter and food to small biting ants. 1. *CECROPIA*.
1. Leaves never peltate, either lobed or not; inflorescences erect, capitate clusters; plants providing internally neither shelter nor food to ants.
 2. Plants terrestrial; seeds large, 1-2 cm in diameter; flowers pedicellate, borne in panicles or umbels; leaves either lobed or entire. 3. *POUROUMA*.
 2. Plants epiphytic; seeds small, about 2 mm in diameter; flowers sessile, borne in dense globose heads; leaves entire. 2. *COUSSAPOA*.

1. *CECROPIA* Loefl.

Hollow-stemmed trees often harboring small vicious ants within the internodes; branch tips short pubescent with stiff uncinat hairs and therefore scabrous; trunk with prop roots. *Leaves* peltate and deeply, usually palmately lobed; upper surface of leaf either smooth or scabrous, lower surface puberulent and green to white with short dense cobwebby pubescence; petioles usually longer than the blades; the base densely tomentose and with waxy food bodies. *Inflorescence* of 4-18 spikes borne on a common peduncle within a cauducous spathe, axillary and paired; *staminate inflorescences* usually somewhat shorter and often more numerous than the pistillate but otherwise the spikes of the different sexes outwardly very similar. *Staminate flowers* with 2 anthers; *pistillate flowers* with 1 stigma. *Fruit* a minute achene.

The genus contains approximately 60 species, most of them South American, but even the commonest are poorly represented in herbaria.

KEY TO THE SPECIES

1. Flowering spikes 8-10 cm long, yellow; leaves with 7-9 deeply pleated lobes, the upper surface smooth

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- at or near maturity (scabrous in juveniles); tall plants mostly of primary forest. 1. *C. insignis*.
 1. Flowering spikes 12–40 cm long, greenish gray; leaves with 9–15 flat or slightly pleated lobes, the upper surface scabrous; medium sized trees abundant in secondary woods. 2. *C. obtusifolia*.

1. *Cecropia insignis* Liebm.

Trees 15 to 30 m tall; bark rough and reddish. *Leaf* blades about 40–100 cm in diameter with 7–8 major veins; midleaf secondary veins often over 2 cm distant, and averaging about 1.5 cm apart; leaf surface distinctly pleated along the lateral veins, smooth above (scaberulous in juveniles) the lower surface usually white with matted arachnoid pubescence; petioles 40–90 cm long. *Staminate and pistillate inflorescences* similar in size, 6–12 cm long, 7–12 mm thick, yellow. *Fruits* 2–2.5 mm long. Flowering December to June; fruiting into September. Nicaragua south into Colombia.

This is the less common of the two species of *Cecropia* at La Selva and is more likely to be found in light gaps in primary forest. The relatively short, stout inflorescences and the fewer lobed, pleated and nonscabrous mature leaves help distinguish it from *C. obtusifolia*. The major secondary veins are also more widely spaced than in the latter species. Because leaf pubescence, degree of scabrosity and leaf lobing is quite variable between individuals and with age, as well as between species, correct determination of vegetative materials can be difficult even at La Selva where only two species occur.

2. *Cecropia obtusifolia* Bertol.

Trees 10–20 m tall, surface of trunk light to dark gray. *Leaf* blades about 40–80 cm in diameter, usually with 10–13 primary veins; secondary veins usually about 1 cm apart and seldom over 2 cm; leaf surface plane, not pleated, very scabrous above, the lower surface usually minutely puberulent or sometimes arachnoid pubescent; petioles 25–70 cm long. *Staminate inflorescences* 8–22 cm long, about 3.5 mm thick, 12–18 spikes per peduncle; *pistillate inflorescences* 18–50 cm long by 0.3–0.6 cm thick (1 cm in fruit), 3–5 spikes per peduncle. *Fruits* about 2 mm long. Flowering and fruiting throughout the year. Throughout the New World tropics.

Very common at La Selva especially in the successional plots and in secondary thickets and clearings on the Western Annex. It is the more commonly encountered *Cecropia* at La Selva although it is seldom found in light gaps in the forest. *Cecropia obtusifolia* is most easily distin-

guished from *C. insignis* by its scabrous and more deeply lobed blades.

2. *COUSSAPOA* Aubl.

Epiphytic shrubs or trees, sometimes strangling and becoming free standing trees; sap resinous, yellowish. *Leaves* simple, entire, elliptic to cordate-ovate, venation pinnate but with 1–3 pairs of palmate basal veins, tertiary veins very prominent below; stipules densely pubescent; petioles commonly $\frac{1}{5}$ – $\frac{1}{3}$ the length of the blade. *Inflorescences* more or less pedunculate, usually branched, densely flowered capitate clusters, similar in both sexes but often somewhat less branched and fewer flowered in the pistillate. *Staminate flowers* with 4 tepals; stamens with 4–6 thecae on a common filament; *pistillate flowers* with the tepals fused throughout, leaving only a small apical aperture, stigma penicellate. *Fruits* somewhat succulent, small.

Coussapoa is restricted to the New World tropics. The genus contains perhaps as many as 50 species, mostly South American. Five species were recognized in *Flora Costaricensis*.

As with many other groups of woody epiphytes, the systematics of *Coussapoa* is poorly resolved. All five of the collections in this genus from La Selva are from pistillate individuals. The morphology and phenology of the inflorescences in this group suggest wind pollination and bird or bat dispersal.

KEY TO THE SPECIES

1. Pistillate inflorescences sessile or on peduncles less than 1 cm long, unbranched; leaf blades oblong, widest at or above the middle, very scabrous above; stipule scars perpendicular to stem axis. 1. *C. nymphaeifolia*.
1. Pistillate inflorescences on peduncles 2–10 cm long, usually bifurcate; leaf blades ovoid to deltoid, widest below the middle, smooth above or very slightly scaberulous; stipule scars diagonal and zig-zag. 2. *C. villosa*.

1. *Coussapoa nymphaeifolia* Standl.

Epiphytic shrubs or trees, the branches 2–10 cm long. *Leaf* blades oblong, 15–35 cm long by 10–22 cm wide, widest at or above the middle; apex broadly acute to rounded, the base rounded and cordulate or broadly cordate with the lobes extending 1–2 cm below the apex of the petiole; lateral veins 9–12 pairs; leaf surface scabrous but otherwise nearly glabrous above, lower surface short erect pubescent with arachnoid pubescence mostly restricted to the leaf margin; petioles 4–7 cm long; stipules 2–8 cm long, bearing 2 longitudinal ridges abaxially. *Staminate inflo-*

rescence much branched, 2–5 cm long, the ultimate heads about 3 mm in diameter; rachis hirsute pubescent; *staminate flowers* each with a single elongate filament 1–1.5 mm long bearing 6 thecae. *Pistillate inflorescence* unbranched, on a stout peduncle 0–0.4 mm long, the heads 1–2 cm in diameter at anthesis; *pistillate flowers* apically very densely covered with pinkish hairs, the stigmas erose, wooly brown pubescent. *Fruits* about 3 mm long. Flowering in April and probably earlier; fruiting by May. Costa Rica.

Known from only two collections in the vicinity of La Selva and from very few collections in all of Costa Rica.

2. **Coussapoa villosa** Poepp. & Endl.
(= *C. panamensis* Pittier)

Epiphytic trees or shrubs, rarely free standing to 30 m tall, bark light gray, sap clear but yellowish. *Leaf* blades elliptic or usually deltoid, 17–25 cm long by 12–19 cm wide, the apex broadly acute, the base rounded, truncate or cordate; lateral veins 14–16 pairs; leaf surface smooth and glabrous above, the lower surface with short erect pubescence but mostly obscured by the white matted arachnoid pubescence; petioles 4–7 cm long; stipules 3–10 cm long, conical, leaving diagonal scars. *Staminate inflorescences* about 3–5 cm long, much branched and the ultimate heads about 5 mm in diameter; rachis densely tan pubescent; *staminate flowers* with a single short (0.1–0.2 mm) filament bearing 3–4 thecae. *Pistillate inflorescences* 4–11 cm long, usually once branched and bearing 2 heads but occasionally unbranched, the heads 2–3.5 cm in diameter; *pistillate flowers* apically very minutely grayish green pubescent, stigmas erose and wooly brown pubescent. Inflorescence green externally with somewhat succulent orange flesh within. *Fruit* an oblong achene ca. 2.5 mm long, imbedded in yellowish mucilage, the surface pitted. Flowering and fruiting specimens from February, May and October; probably flowering throughout the year. Southern Mexico south into northwestern South America.

Most often found in the alluvial forest at La Selva along the Río Puerto Viejo. All of the collections known so far from La Selva are pistillate suggesting that the female plants are somehow more conspicuous or accessible than male plants.

3. **POUROUMA** Aubl.

Trees 20–30 m tall; surface of bark usually dark reddish brown, the trunk often with buttresses but lacking stilt roots. *Leaves* simple and entire or deeply palmately lobed, smooth or sca-

brous above, the lower surface masked (except for the veins) by a white, densely matted arachnoid pubescence; petioles $\frac{1}{3}$ – $\frac{3}{4}$ the length of the blade; stipules glistening sericeous; stipule scars perpendicular to the branch axis. *Staminate inflorescences* much branched, many flowered; flowers 3- or 4-parted, tepals lanceolate, fused at the base, filaments separate. *Pistillate inflorescences* few- to many-flowered, the branching less profuse; flowers tubular, the perianth persistent and completely enclosing the fruit except for the small styler opening; stigma large, discoid, lobed, densely brown pubescent. *Fruits* relatively large, the persistent perianth becoming somewhat succulent.

Pourouma is primarily a South American genus of 30–50 species only two of which range as far north as Costa Rica. At La Selva the plants are not known to be epiphytic although they are reportedly so elsewhere.

KEY TO THE SPECIES

1. Leaves mostly deeply 4–6-lobed, strikingly scabrous above. 1. *P. aspera*.
1. Leaves entire, never scabrous above. 2. *P. minor*.

1. **Pourouma aspera** Trecul
(= *P. johnstonii* Woodson)

Trees 15–30 m tall; trunk dark reddish brown; branchlets glabrous. *Leaf* blades mostly deeply 4–6 palmately lobed and veined, (12)15–40(50) cm long and (10)20–30(40) cm wide, leaf surface very scabrous above, pleated between the lateral veins, lower surface (especially along the veins) with shiny tan appressed hairs 0.5–1.0 mm long, the surface apparently glaucous; petioles 10–28 cm long; stipules about 6 cm long, minutely appressed pubescent with hairs 0.1–0.2 mm long; stipule scars perpendicular to the branch. *Staminate inflorescences* much branched, 10–28 cm long; rachis densely appressed pubescent; staminate flowers congested. *Pistillate inflorescences* much branched, 10–15 cm long (in fruit); rachis densely reddish brown puberulent; *pistillate flowers* 3–7 mm long, in cymose clusters at the ends of the inflorescence branches. *Fruits* ovoid, 1–2 cm long, minutely erect pubescent and therefore scabrous, reddish brown. Flowering probably at the end of the dry season, April to June, fruits maturing July to October. Honduras south into northern South America.

Widespread in the forest at La Selva. Although its overall growth form and leaf shape are reminiscent of *Cecropia*, *P. aspera* grows mostly in primary forest rather than in gaps or secondary woods. The reddish brown, buttressed trunk and

nonpeltate leaves serve to distinguish it from species of *Cecropia*.

The degree of lobing of the leaves is quite variable even on the same plant. Most leaves are deeply 4–6-lobed but juvenile leaves and those near the inflorescence may be shallowly 3-lobed or even unlobed. Even the juvenile leaves are very scabrous, more so than any other species in the family at La Selva. The large persistent orange or tan stipules help distinguish the seedlings and young saplings of this species.

2. ***Pourouma minor*** Benoist
(= *P. umbellifera* Burger)

Trees 20–35 m tall; branchlets sericeous pubescent with silvery gray hairs. *Leaves* elliptic, unlobed, 16–23 cm long by 8.5–11 cm wide, bearing 2 glandular spots along the midrib at the petiole; the blade distinctly pleated; upper surface glabrous except for appressed hairs on the midrib and margin; lower surface white, obscured by the matted arachnoid pubescence and

also appressed sericeous on the veins; petioles 5–7 cm long, silvery appressed pubescent and hirsute; stipules 4–11 cm long, densely silvery pubescent. *Staminate inflorescence* much branched, 6–8 cm long; the flowers pedicellate. *Pistillate inflorescence* unbranched, the peduncle 4–7.5 cm long, silvery tan appressed pubescent; *pistillate flowers* about 1 cm long, 3–7 clustered and sessile at the tip of the peduncle. *Fruits* turbinate, about 2 cm long by 1.5 cm wide, green, minutely puberulent. Flowering probably throughout the year; fruiting collections in April. Costa Rica south into northern South America.

Scattered on slopes and ridges throughout the primary forest. Its narrowly elliptic leaves, which are smooth rather than scabrous above, and white below, and the villous pubescent petioles and branchlets distinguish *Pourouma minor* from the rest of the family at La Selva. The species is distinctive and probably common throughout its range but it is very poorly represented in collections.